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The electric organ discharges of the *Petrocephalus* species (Teleostei: Mormyridae) of the Upper Volta System

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In this study, a first comparative investigation of all four species of *Petrocephalus* (*P. bovei*, *P. bane*, *P. soudanensis* and *P. cf. pallidomaculatus*) present in the Upper Volta system and their electric organ discharges (EOD) was conducted. It was found that *P. bovei* was the most widespread (in terms of habitat use), but in several places *P. bovei*, *P. soudanensis* and *P. cf. pallidomaculatus* occurred syntopically. All species emitted a triphasic signal, and with very few exceptions, the *Petrocephalus* species of the Upper Volta system could clearly be identified on the basis of their EOD waveforms. The most obvious differences between species in EOD waveforms were in amplitude of the last phase, total duration and fast Fourier transformation (FFT) peak frequency. No sexual dimorphism was present in the EOD of any species although external dimorphism, *i.e.* an indentation at the base of the anal fin of mature males, was common. The EOD waveform diversity in the Upper Volta principally resembled that found in four sympatric *Petrocephalus* species from the Ogooué system (Gabon) and might play a role in species recognition and speciation processes.

Key words: communication; EOD waveform; Pendjari; speciation; weakly electric fish; West Africa.

INTRODUCTION

Approximately 30 species of *Petrocephalus* are currently recognized. They have been placed into their own subfamily, the Petrocephalinae, based on morphological characters (Taverne, 1969, 1972). Monophyly of the Petrocephalinae has been confirmed by more recent molecular studies designating them as sister group of all other mormyrids, the subfamily Mormyrinae (Alves-Gomes & Hopkins, 1997; Lavoué *et al.*, 2000; Sullivan *et al.*, 2000). All members of the

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family Mormyridae live in African freshwater systems and are weakly electric. They possess a specialized electric organ that produces electric organ discharges (EOD) used for orientation and communication (Moller, 1995; Hopkins, 1999*a*, *b*). The waveform of the EOD is species specific and sometime sex specific (Westby & Kirschbaum, 1982; Hopkins, 1999*a*, *b*). It depends on the morphology of the electric organ and thus does not change within short periods of time. Nevertheless, relatively slow changes of EOD waveform are known to occur during development (Kirschbaum, 1995) and depending on the hormonal state of the animal, especially in males during the mating season (Carlson *et al.*, 2000).

Weakly electric fishes are mainly nocturnal and use their EODs for actively probing their environment. Mormyrids cannot only detect and localize objects through electrolocation but also perceive additional object variables such as size, shape and electric impedance (von der Emde, 1999, 2004, 2006; von der Emde & Schwarz, 2002). EODs also play a crucial role during electro-communication. It has been shown that at least some mormyrids can recognize the EODs of their own species (Hopkins & Bass, 1981; Graff & Kramer, 1992) as well as the opposite sex (Hopkins & Bass, 1981). For several species, there is some evidence that females may choose their mates at least partly on the basis of EOD features and that EOD waveform may be an important mate-recognition trait during the evolution of new species. To mention an example, Sullivan *et al.* (2002) and Arnegard & Hopkins (2003) focused on sympatric *Brienomyrus* species from Gabon and showed that morphological similar taxonomic units can be discriminated by EOD characteristics. These studies assume that EOD waveform plays a role in speciation processes.

In this study, EOD waveforms of four sympatric *Petrocephalus* species from the Upper Volta system were described and compared to each other. Within this genus, EODs may also play a role in species recognition during nocturnal spawning and, in the long term, in species isolation during evolution. A prerequisite for this hypothesis is that EODs are distinctive among potentially interbreeding species in features coded and discriminated by the electrosensory system of mormyrids. The present study tested this hypothesis for the *Petrocephalus* of the Upper Volta by documenting EOD features that could be the basis for species discrimination. In addition, an investigation was made of how EOD waveforms may serve as possible species isolating signals. The variability in EOD waveforms within and between sampling locations has been discussed elsewhere for *Petrocephalus bovei* (Valenciennes) (Moritz *et al.*, 2008).

MATERIALS AND METHODS

For EOD recording, specimens of *Petrocephalus* spp. were caught in the Pendjari region, Benin, and the Mou-Houn region (formerly Black Volta), Burkina Faso, between February and May 2005 using small seines, dip nets and basket nets. Sampling localities are given in Fig. 1. Species identification followed Bigorne & Paugy (1991). EODs from 314 specimens from these study areas have been analysed for this investigation. Additional 17 *Petrocephalus pallidomaculatus* Bigorne & Paugy were caught in the Ouémé system (Benin) for comparison with *Petrocephalus cf. pallidomaculatus* from the Volta basin (Fig. 1). Standard length (L_S) and the status of the anal fin complex were noted because sexually active males of mormyrids show a typical indentation of the ventral body wall above the anal fin (Moller *et al.*, 2004). Detailed meristic

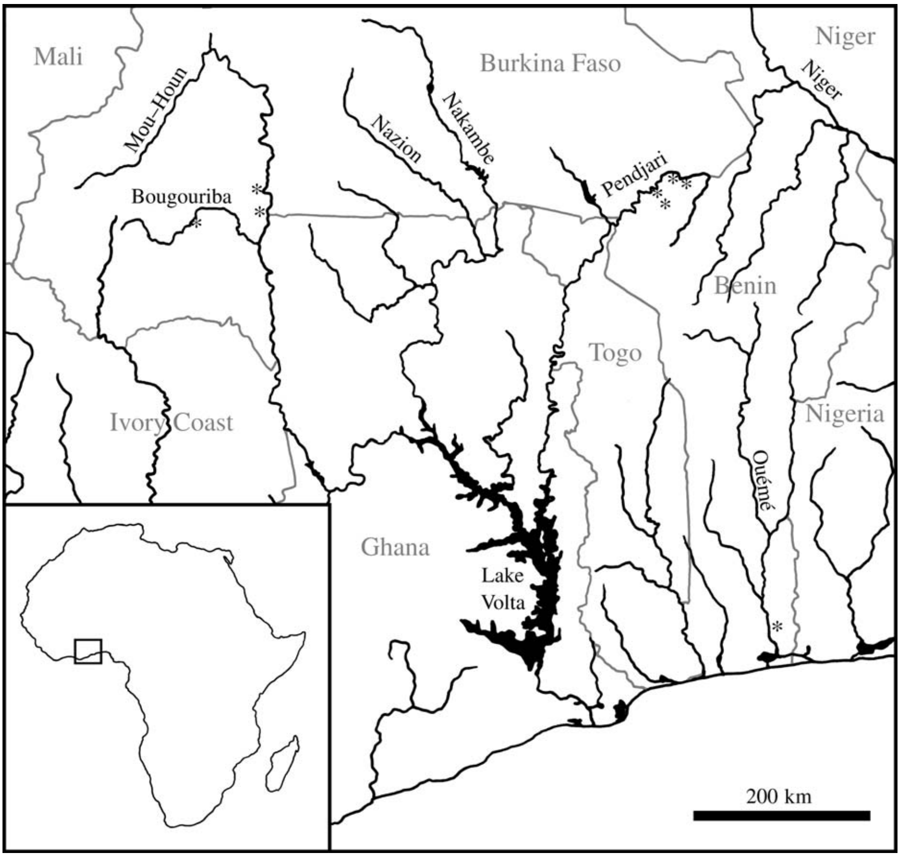

FIG. 1. Overview of the study area (*, sampling sites). For clarity, not all sampling points in the Pendjari region are shown.

measures were only taken from 52 *P. cf. pallidomaculatus* and 38 *P. pallidomaculatus* using a digital calliper.

EODs were recorded shortly after specimen collection in a 12 l plastic tank filled with water from the sampling site. An SDS 200 digital oscilloscope (200 MHz, 5GS s^{-1}; Soft DSP, Seoul, South Korea) together with an additional amplifier (custom made, electric shop University of Bonn) were used. All EODs were recorded with the head pointing to the positive electrode. To analyse the EODs, 'R' (R-project; www.R-project.org) was used, running a custom-made measuring programme.

The beginning and end of a signal were defined for this study to be 1·5% deviation from the averaged zero line with respect to the overall peak-to-peak amplitude range, *i.e.* from the positive to the negative amplitude maximum of the EOD (Fig. 2). Single phases within a signal are separated by crossing the zero line. Total length of the EOD and of each phase, the maximum phase amplitudes relative to the total EOD amplitude, and the area of each phase were also measured. The naming of the phases (Fig. 2) was developed to ease comparisons with other genera in future investigations. A fast Fourier transformation (FFT) was conducted for each signal and the frequency of maximum amplitude was determined (FFT-peak). The setting of an amplitude threshold for determining the beginning and the end of EOD phases was necessary to deal with unavoidable electrical noise. In some cases, this may eliminate information, leading, for example, to a shorter total EOD duration than the real duration. The description of

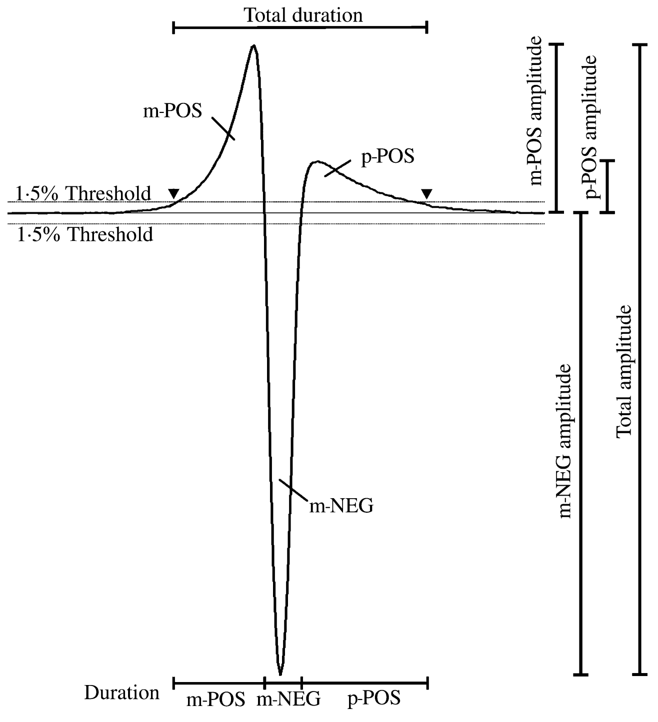

FIG. 2. Variables used for the characterization of the electric organ discharges (EOD) in this study. Here, an example of a *Petrocephalus bovei* EOD is shown. The main positive phase (m-POS) corresponds to P1 in Lavoué *et al.* (2004), the main negative phase (m-NEG) to P2 and the posterior positive phase (p-POS) to P3.

the EOD waveform, however, is usually not affected by this procedure. Setting a threshold is also necessary to perform quantitative comparisons between EODs. Problems may arise when EOD-phases of very low amplitude fall below the threshold criterion and thus will be counted as not present, which will bias, for example, tests for normality. In this investigation, this happened only once in a single *P. pallidomaculatus*, where a posterior positive amplitude (p-POS) was visible in the EOD waveform but not counted because its amplitude fell below the 1·5% threshold criterion. Thus, the interpretation of the results were only slightly effected.

Statistical tests were only performed for groups, *i.e.* individual fish from one location for each species, if at least six individuals for the respective group had been recorded. In order to compare the measured EOD variables an univariate analysis (ANOVA) was performed using SPSS (SPSS Inc., Chicago, IL, U.S.A.). As variance of EOD variables may differ between sampling locations in mormyrids (Moritz *et al.*, 2008) the Games–Howell test, which is insensitive for different variances, was used as a *post hoc* test. All variables with significant differences ($P < 0{\cdot}001$) were used in a following principal component analysis (PCA) using palaeontological statistics (PAST); (Hammer *et al.*, 2001). Loadings for variables are given below in the respective figure. All the variables were used in this analysis, although they are probably dependent on each other, as wave form in this type of EOD may depend mathematically on only very few parameters (Westby, 1984). The focus of this study, however, focuses on waveform differences, which may be important for species recognition in *Petrocephalus* and each of the used variables has the potential to play a role in this issue.

Values are always given as mean ± S.D. Several specimens collected for this investigation have been deposited in the Natural History Museum London (BMNH), see Appendix.

RESULTS

Four species of *Petrocephalus* were found in the Upper Volt basin (Fig. 3), of which *P. bovei* is by far the most common, followed by *P. cf. pallidomaculatus*, *Petrocephalus soudanensis* Bigorne & Paugy and finally *Petrocephalus bane* (Lacepède). All *Petrocephalus* spp. investigated produced a triphasic EOD (Figs 3 and 6) with a strong first head-positive phase (m-POS), followed by a negative phase (m-NEG), which was about two to three times the amplitude of m-POS. The third (positive) phase (p-POS) was always smaller than m-POS and its

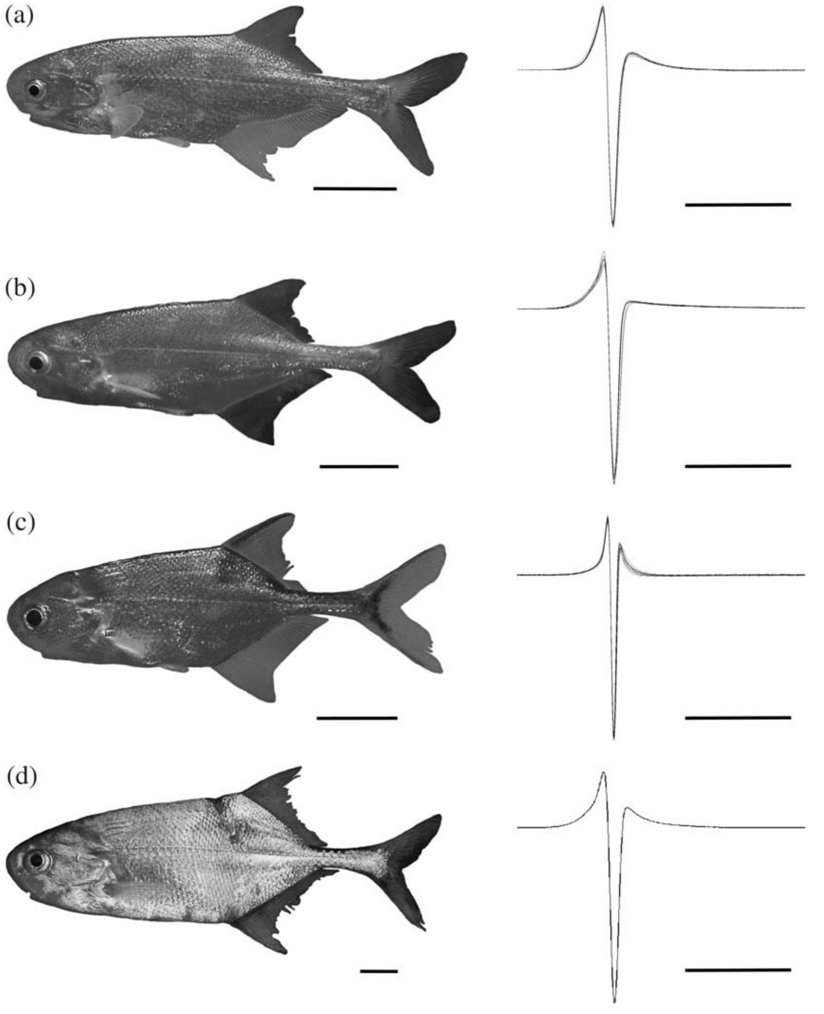

FIG. 3. Live specimens of *Petrocephalus* and overlay of electric organ discharges (EOD) from the first 10 recorded specimens from different locations, except for *Petrocephalus bane* (only one EOD). (a) *Petrocephalus bovei*, EODs from the Pendjari River close to Mare Tiabiga, (b) *Petrocephalus cf. pallidomaculatus*, EODs from Mou-Houn at Ouessa, (c) *Petrocephalus soudanensis*, EODs from Mou-Houn at Ouessa and (d) *P. bane*, injured by getting stuck in a net, single EOD from Pendjari River at Camping Elephant. Scales for specimens 10 mm; scale for EODs 100 μs.

Compared with	Variable	*P. bovei*	*P. soudanensis*	*P. cf. pallidomaculatus*
P. soudanensis	Dur. EOD	**		
	Dur. m-POS	**		
	Dur. m-NEG	**		
	Dur. p-POS	**		
	Amp. m-POS	*		
	Amp. p-POS	**		
	Area m-POS	**		
	Area m-NEG	**		
	Area p-POS	**		
	FFT peak	**		
P. cf. pallidomaculatus	Dur. EOD	NS	**	
	Dur. m-POS	**	**	
	Dur. m-NEG	**	**	
	Dur. p-POS	**	**	
	Amp. m-POS	**	**	
	Amp. p-POS	**	**	
	Area m-POS	NS	**	
	Area m-NEG	*	**	
	Area p-POS	**	NS	
	FFT peak	**	**	
P. pallidomaculatus	Dur. EOD	NS	**	NS
	Dur. m-POS	**	**	NS
	Dur. m-NEG	NS	**	NS
	Dur. p-POS	*	**	NS
	Amp. m-POS	NS	NS	**
	Amp. p-POS	**	**	NS
	Area m-POS	NS	**	NS
	Area m-NEG	NS	**	*
	Area p-POS	**	NS	NS
	FFT peak	**	**	NS

FIG. 4. Summary of results from statistical analysis comparing electric organ discharge (EOD) variables (see Fig. 2) of *Petrocephalus bovei* (n = 168), *Petrocephalus soudanensis* (n = 52), *Petrocephalus cf. pallidomaculatus* (n = 94) and *Petrocephalus pallidomaculatus* (from Ouémé) (n = 17). Displayed variables have been tested to be significant (all $P < 0{\cdot}001$) by univariate analysis (ANOVA). *, $\alpha = 0{\cdot}05$; **, $\alpha = 0{\cdot}001$ (Games–Howell *post hoc* tests; significant values are grey shaded). Dur., duration; Amp., amplitude in per cent of total EOD amplitude; FFT, fast Fourier transformation; NS, not significant.

characteristic waveform was species specific. All *Petrocephalus* EODs were rather short in duration, lasting from 100 to 300 μs.

The *Petrocephalus* spp. investigated showed a sexual dimorphism at the base of the anal fin, *i.e.* a dorsally directed indentation of the posterior body wall in mature males, as described for several other mormyrid species (Daget & Durand, 1981; Pezzanite & Moller, 1998; Moller *et al.*, 2004; Greisman & Moller, 2005). Whether this sexual dimorphism disappears seasonally during non-reproductive periods could not clearly be assessed on the basis of the present data. Specimens showing an anal fin indentation, however, were caught throughout the entire field period, which lasted from October to May, corresponding to a time period from the end of the rainy season to the start of the next rainy season.

For all *Petrocephalus* species, several specimens of the same species were often caught in the same catch. This indicates that they, at least from time to time, form monospecific shoals. On the other hand, at certain locations such as isolated overhanging root systems, two or three species of *Petrocephalus* could be found in a single catch, showing that several species can live very close together even inhabiting the same microhabitat. To refer to this situation, the term 'syntopic' is used in this study.

PETROCEPHALUS BOVEI

The 168 specimens of *P. bovei* were 53·8 ± 11·7 mm L_S (range from 25 to 92 mm L_S). The species had a uniform light silvery colouration; only the mid-dorsal line and the dorsal half of the head were sometimes darker, slightly olive or golden. The fins were usually transparent; occasionally the unpaired fins were slightly yellow and sometimes the distal margin of the dorsal fin and upper lobe of the caudal fin were blackish. A sexual dimorphism at the base of the anal fin was seen in males >50 mm L_S.

Petrocephalus bovei is the most common species of this genus within the Upper Volta system and can be found in all its tributaries. It inhabits most aquatic habitats accessible for fishes. In this investigation, the species was found at all sampling habitats, *i.e.* in small temporary streams ('marigots'), in 'mountain' streams at the Atakora Chain in northern Benin and in the rivers and lakes of different sizes. In the three study sites in the Mou-Houn region and in one site at the Pendjari River (Pont Arly), the species occurred syntopically with *P. soudanensis* and *P. cf. pallidomaculatus*. The last species was additionally caught together with *P. bovei* in the Pendjari River close to the Mare Sacre and within the Mare Tiabiga, a lake in adjacent to the Pendjari River.

The detailed characteristics of the *P. bovei* EODs are listed in Table I, and a specimen and EOD waveforms from the first 10 specimens caught at the Mou-Houn or the Pendjari are displayed in Fig. 3(a). EODs of this species lasted for 271 ± 55 μs, with a distinct p-POS having an amplitude of 7·9 ± 1·3% of the total EOD amplitude. The FFT-peak was at 8873 ± 1397 Hz. There was a negative correlation between L_S and EOD duration for all *P. bovei* sampled in this investigation (Pearson correlation test, $r = -0{\cdot}739$, $P < 0{\cdot}001$, $n = 154$), showing that larger specimens had shorter pulses. Tests for single locations, however, were significant only once, *i.e.* at the Volta at Ouessa (Pearson correlation test, $r = -0{\cdot}351$, $P < 0{\cdot}05$, $n = 50$). A correlation between sex and EOD length could not be detected (*t*-test, $P > 0{\cdot}05$, for specimens ≥50 mm L_S, $n = 103$ with 40 distinct males). In addition, there was also no correlation between sex and p-POS amplitude (*t*-test, $P > 0{\cdot}05$) or any other measured EOD feature.

PETROCEPHALUS BANE

Petrocephalus bane was the largest species investigated up to 183 mm L_S (Daget & Durand, 1981). Five specimens caught in this investigation in the

TABLE I. Characteristics of 168 electric organ discharges (EOD) from *Petrocephalus bovei* (see Figs 1 and 2)

Location	*n*	Dur. EOD (μs)		Dur. M-POS		Dur. m-NEG		Dur. p-POS		Amp. m-POS		Amp. p-POS		FFT-peak (Hz)	
		Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
Bougouriba Dan	7	270 ± 21	242–306	95 ± 7	90–106	37 ± 4	34–40	138 ± 17	116–170	22·8 ± 3·2	18·7–29·1	8·9 ± 0·5	8·0–9·5	8301 ± 994	6836–10010
Volta Fitingue	4	278 ± 15	266–298	94 ± 3	92–98	40 ± 1	38–40	145 ± 15	134–166	25·1 ± 1·5	23·4–26·8	8·4 ± 1·1	7·6–10·0	8270 ± 461	7812–8911
Volta Ouessa	50	277 ± 34	230–348	96 ± 13	78–126	38 ± 7	30–62	143 ± 16	114–178	24·1 ± 1·7	20·6–27·7	8·0 ± 1·0	4·6–10·8	8955 ± 1551	5615–11352
Biakou	6	345 ± 34	312–410	104 ± 10	94–122	48 ± 12	40–72	193 ± 14	174–216	22·2 ± 1·3	20·2–23·6	6·6 ± 1·3	4·6–8·1	7650 ± 1046	5615–8545
Mare Bori	25	358 ± 33	312–428	107 ± 10	92–124	50 ± 6	38–66	202 ± 31	158–264	24·1 ± 2·1	21·3–29·6	7·0 ± 1·5	4·6–12·1	7192 ± 658	6104–8179
Mare Yanguali	6	259 ± 12	248–278	89 ± 3	84–92	35 ± 2	32–38	135 ± 8	126–148	23·3 ± 1·3	21·9–25·6	7·1 ± 0·8	6·1–8·4	9318 ± 676	8423–10254
Pendjari at M. Sacre	9	297 ± 12	276–312	100 ± 4	94–108	42 ± 3	38–46	155 ± 7	144–162	24·5 ± 1·1	23·1–26·0	6·2 ± 0·6	5·0–6·9	8226 ± 680	7202–9155
Pendjari Ponte Arly	2	285 ± 21	270–300	101 ± 10	94–108	39 ± 4	36–42	145 ± 7	140–150	24·3 ± 0·1	24·2–24·4	6·5 ± 0·3	6·2–6·7	8057 ± 1381	7080–9033
Mare Diwouni	25	202 ± 12	182–238	73 ± 4	68–86	30 ± 2	26–38	99 ± 7	86–114	22·6 ± 0·8	20·9–24·3	8·9 ± 0·6	7·6–10·2	10259 ± 561	8545–11353
Mare Tiabiga	22	229 ± 17	204–280	80 ± 4	72–88	33 ± 2	30–40	116 ± 13	98–162	25·6 ± 1·4	22·1–28·0	8·6 ± 1·4	7·0–13·9	9849 ± 665	8300–10986
Pendjari at M. Tiabiga	12	234 ± 10	224–256	77 ± 4	72–84	40 ± 1	38–42	117 ± 7	110–132	28·7 ± 0·9	27·4–30·2	7·6 ± 0·5	6·5–8·2	8911 ± 325	8179–9399
All together	168	271 ± 55	182–428	91 ± 15	68–126	39 ± 8	26–72	142 ± 36	86–264	24·3 ± 2·2	18·7–30·2	7·9 ± 1·3	4·6–13·9	8873 ± 1397	5615–11353

Amp., amplitude of phase in per cent of total EOD amplitude; Dur., duration; FFT, fast Fourier transformation.

Pendjari River at Camping Elephant were 91·0 ± 12·9 mm (range from 77 to 106 mm L_S). The species had a uniform silvery-grey colouration, but dark on the mid-dorsal line, especially at the caudal peduncle. The fins were transparent; only the first rays of the dorsal fin and the base of the caudal fin were blackish. One of the specimens collected had an indentation at the base of the anal fin, but less pronounced than in the other species.

Only a single specimen (101 mm L_S) was caught alive in the leading net of a basket trap [Fig. 3(d)]. Its EOD lasted for 248 μs, with m-POS lasting for 98 μs, m-NEG for 36 μs and p-POS for 114 μs. The amplitude of m-POS was 24·1% and that of p-POS 8·9% of the total EOD amplitude. The maximum frequency of the FFT was at 8179 Hz. During this study, no other *Petrocephalus* species had been caught at this particular location, but all the other three species were recorded in the Pendjari River only a few kilometres away.

The EODs of the single *P. bane* specimen were not distinguishable from the EODs of *P. bovei* when all *P. bovei* individuals across all sampling locations were considered. When only comparing the *P. bane* EOD with the EODs of those *P. bovei* co-occurring at close-by locations in the Pendjari River, however, possible differences between the EODs become apparent. The duration of the negative phase (m-NEG) of the *P. bane* EOD (32 μs) was slightly shorter than that of the *P. bovei* EOD (36·5 ± 2·1 μs, range from 34 to 40 μs, n = 22). In addition, the m-NEG amplitude of the *P. bane* EOD (75·9%) was close to the maximum of the range of the *P. bovei* EODs (73·3 ±2·4%, range from 69·8 to 76·9%, n = 22). Also, the relative amplitude of p-POS was higher in *P. bane* (8·9%) than in *P. bovei* (7·0 ± 0·8%, range from 5·0 to 8·2%, n = 22). These numbers may suggest that the signals of *P. bane* and *P. bovei* may differ when the two live syntopically. EODs from more specimens of *P. bane*, however, are necessary before any conclusions can be drawn.

PETROCEPHALUS SOUDANENSIS

Petrocephalus soudanensis has about the same size as *P. bovei*, 55·5 ± 9·1 mm (range from 31 to 73 mm L_S, n = 52). Compared with *P. bovei* the species had a higher body and a larger eye. *Petrocephalus soudanensis* was the only species of this region with clear colour patterns as described in Bigorne & Paugy (1991). That is, they had a black spot below the anterior base of the dorsal fin, black stripes on the first dorsal fin rays, along the dorsal fin base, the dorsal part of the caudal peduncle and on the superior and inferior border of the caudal fin [Fig. 3(c)]. This description can be supplemented based on the specimens of the present study: the base of the caudal fin was black and in the males the indentation of the posterior body wall at the base of the anal fin was accentuated by a black stripe.

Petrocephalus soudanensis was found in rivers, *i.e.* the Bougouriba, the Mou-Houn and the Pendjari, usually in areas with big stones and lots of burrows but also in dense plant 'tangles' such as root networks. In all places, where *P. soudanensis* was found, *P. bovei* and *P. cf. pallidomaculatus* occurred also syntopically.

Table II summarizes the characteristics of this species' EOD, and Fig. 3(c) shows a specimen and the waveforms of the EODs from the first 10 specimens

TABLE II. Characteristics of 52 electric organ discharges (EOD) from *Petrocephalus soudanensis* (see Figs 1 and 2)

Location	*n*	Dur. EOD (μs)		Dur. m-POS		Dur. m-NEG		Dur. p-POS		Amp. m-POS		Amp. p-POS		FFT-peak (Hz)	
		Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
Bougouriba Dan	13	143 ± 17	120–180	84 ± 11	68–114	19 ± 2	18–24	40 ± 8	26–52	23·9 ± 1·1	22·4–25·6	13·8 ± 2·3	10·8–18·1	19259 ± 1839	15380–21729
Volta Fitingue	3	136 ± 16	122–154	71 ± 2	68–72	21 ± 3	18–24	44 ± 17	32–64	28·6 ± 2·5	25·9–30·8	12·8 ± 1·4	11·4–14·1	18026 ± 3731	14160–21606
Volta Ouessa	26	126 ± 13	108–172	65 ± 7	58–94	18 ± 1	16–20	42 ± 7	24–58	26·4 ± 1·4	23·1–29·3	13·2 ± 1·5	10·3–16·0	20855 ± 1814	15869–23926
Pendjari Ponte Arly	10	148 ± 12	124–162	82 ± 4	74–88	19 ± 2	16–20	48 ± 9	34–60	23·9 ± 1·6	21·0–25·7	13·6 ± 2·1	9·4–16·8	18909 ± 1353	17212–21729
All together	52	135 ± 17	108–182	73 ± 12	58–114	19 ± 2	16–24	43 ± 9	24–64	25·4 ± 2·0	21·0–30·8	13·4 ± 1·8	9·4–18·1	19919 ± 2060	14160–23925

Amp., amplitude of phase in per cent of total EOD amplitude; Dur., duration; FFT, fast Fourier transformation.

from the Mou-Houn at Ouessa. This species emitted the shortest EODs of the four species investigated of this genus resulting in the highest maximum frequencies of the FFT (19 919 ± 2060 Hz). There was no correlation between L_S and EOD length for all *P. soudanensis* of this investigation (Pearson correlation test, $r = -0{\cdot}115$, $P > 0{\cdot}05$, $n = 52$) or for any sampling location. Neither EOD duration nor p-POS amplitude was found to be significantly related to sex in univariate comparisons (*t*-test, both $P > 0{\cdot}05$, for specimens $\geq$50 mm L_S, $n = 38$ with eight distinct males). The EODs of *P. soudanensis* can be easily distinguished from congeners in the Upper Volta. The range of the FFT-peak and duration of m-NEG did not show an overlap to any other species (Tables I–III). Total EOD duration, duration of p-POS and amplitude of p-POS of the *P. soudanensis* EODs scarcely overlapped those of the other species and even less so when the species were examined separately for each location.

PETROCEPHALUS CF. PALLIDOMACULATUS

Petrocephalus cf. pallidomaculatus was of similar size as *P. bovei*, 48·5 ± 5·7 mm (range from 36 to 70 mm L_S, $n = 96$). Body shape and colouration was almost the same as in *P. bovei*, except from a conspicuously larger eye in *P. cf. pallidomaculatus* [Fig. 3(b)]. A sexual dimorphism at the base of the anal fin was present.

Petrocephalus cf. pallidomaculatus was common in rivers (Bougouriba, Mou-Houn and Pendjari), and one school was caught in a lake, Mare Tiabiga, which is connected to the Pendjari River during the rainy season. In most river collection places where *P. cf. pallidomaculatus* was found, *P. soudanensis* has also been collected, whereas *P. bovei* was collected in all localities where *P. cf. pallidomaculatus* occurred.

Table III lists the EOD characteristics of *P. cf. pallidomaculatus*. A specimen and 10 unique EOD waveforms are displayed in Fig. 3(b). The FFT-peak was at 6988 ± 7256 Hz. A correlation between L_S and EOD duration could not be detected in *P. cf. pallidomaculatus* over all locations (Pearson correlation, $r = -0{\cdot}099$, $P > 0{\cdot}05$, $n = 95$) or within any single sampling location. Also, a relationship between sex and EOD length or p-POS amplitude could not be detected (*t*-test, both $P > 0{\cdot}05$, for specimens $\geq$50 mm L_S, $n = 34$ with seven distinct males). In comparison to the other *Petrocephalus* species, *P. cf. pallidomaculatus* had a very low p-POS amplitude. Although p-POS amplitude of the EOD of *P. cf. pallidomaculatus* and those of *P. bovei* showed slight overlap, the shape of p-POS was distinctive in *P. cf. pallidomaculatus*. When p-POS amplitude was plotted with its duration (Fig. 5), both species are separated from each other quite well. Only a few *P. cf. pallidomaculatus* individuals, all being caught in the Mare Tiabiga of the Pendjari region, clustered together with *P. bovei*. If only co-occurring specimens from the Mare Tiabiga were compared, however, the EODs of the two species became clearly separate: in the Mare Tiabiga, there was no overlap between *P. cf. pallidomaculatus* and *P. bovei* in p-POS amplitude, FFT-peak and duration of m-POS (Tables I and III).

PETROCEPHALUS PALLIDOMACULATUS

The identity of *P. cf. pallidomaculatus* (see above) was not definitely ascertained. First, *P. pallidomaculatus* was not recorded from the Pendjari region

TABLE III. Characteristics of 94 electric organ discharges (EOD) from *Petrocephalus cf. pallidomaculatus* (see Figs 1 and 2)

Location	n	Dur. EOD (μs) Mean ± S.D.	Dur. EOD (μs) Range	Dur. m-POS Mean ± S.D.	Dur. m-POS Range	Dur. m-NEG Mean ± S.D.	Dur. m-NEG Range	Dur. p-POS Mean ± S.D.	Dur. p-POS Range	Amp. m-POS Mean ± S.D.	Amp. m-POS Range	Amp. p-POS Mean ± S.D.	Amp. p-POS Range	FFT-peak (Hz) Mean ± S.D.	FFT-peak (Hz) Range
Bougouriba Dan	7	296 ± 16	276–316	112 ± 8	102–120	53 ± 9	42–64	131 ± 25	92–150	17·8 ± 1·9	15·7–20·5	3·5 ± 0·9	2·3–4·6	5929 ± 385	5615–6592
Volta Fitingue	1	252	—	92	—	42	—	118	—	20·0	—	3·0	—	7080	—
Volta Ouessa	32	252 ± 19	2114–294	92 ± 7	82–106	41 ± 3	36–48	119 ± 16	86–158	22·4 ± 2·0	19·0–26·0	3·2 ± 0·5	2·3–4·9	7595 ± 635	6714–9766
Pendjari at M. Sacre	11	271 ± 28	224–338	107 ± 9	94–130	44 ± 4	38–52	120 ± 20	86–156	21·8 ± 1·8	19·0–24·3	3·0 ± 0·5	2·5–3·9	6625 ± 538	5371–7568
Pendjari Ponte Arly	31	264 ± 22	222–334	109 ± 9	98–136	46 ± 4	40–60	110 ± 20	48–170	20·3 ± 2·0	15·2–24·5	3·0 ± 0·5	1·6–6·5	6667 ± 425	5615–7446
Mare Tiabiga	12	249 ± 25	216–302	108 ± 6	100–118	37 ± 3	32–42	104 ± 20	78–148	21·1 ± 1·5	18·5–23·3	3·3 ± 0·8	2·6–5·5	7141 ± 484	6348–8057
All together	94	261 ± 24	214–338	103 ± 11	82–136	43 ± 6	32–64	115 ± 20	48–170	21·1 ± 2·3	15·2–26·0	3·1 ± 0·7	1·6–6·5	6988 ± 7256	5371–9766

Amp., amplitude of phase in per cent of total EOD amplitude; Dur., duration; FFT, fast Fourier transformation.

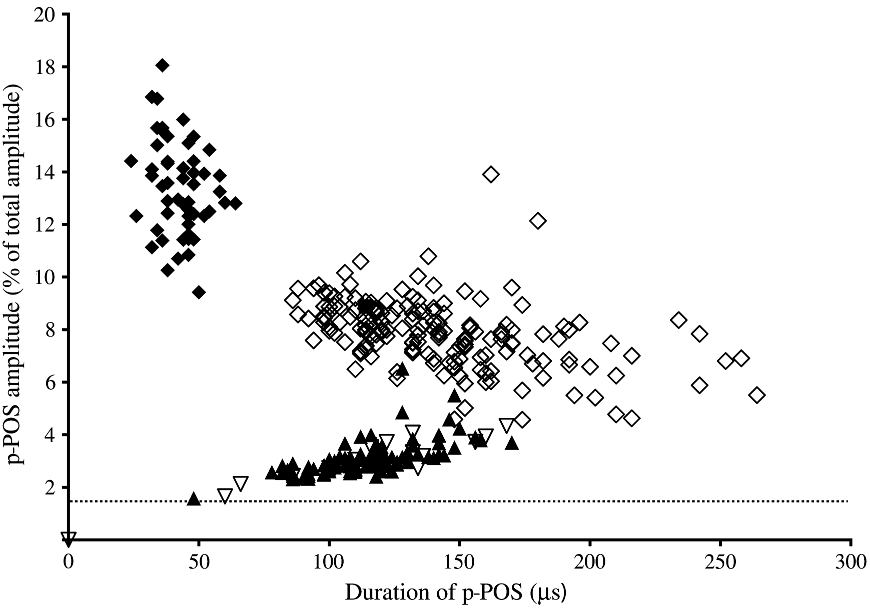

FIG. 5. Scatterplot of the relative amplitudes of p-POS and the durations of p-POS (see Fig. 2) for *Petrocephalus bovei* (◇, $n = 168$), *Petrocephalus soudanensis* (◆, $n = 52$), *Petrocephalus bane* (■, $n = 1$) and *Petrocephalus cf. pallidomaculatus* (▲, $n = 94$) from the Upper Volta, and *Petrocephalus pallidomaculatus* (▽, $n = 17$) from the Ouémé. The 1·5% amplitude threshold is displayed as a dotted line.

before, and second, the colour pattern especially the diagnostic pallid macula was missing. In order to elucidate this issue, 38 specimens of *P. pallidomaculatus* from outside of the actual study area, *i.e.* from the Ouémé basin, were included in this investigation. These specimens were 47·8 ± 6·1 mm (range from 38 to 63 mm L_S) and were sampled at Hossa at the Ouémé River in southern Benin. Of 17 of these individuals the EODs were recorded. These 17 specimens were 50·1 ± 7·0 mm (range from 42 to 62 mm L_S). *Petrocephalus pallidomaculatus* (from the Ouémé) and *P. cf. pallidomaculatus* (from the Pendjari) did not differ in any meristic nor morphometric measurement (Table IV). Also in colouration, there was little difference, except for the eponymous 'pallid macula', which was slightly visible in some *P. pallidomaculatus* specimens caught in the Ouémé, especially under oblique illumination. This colour pattern was not seen in any of the 94 *P. cf. pallidomaculatus* from the Pendjari region. Eight *P. pallidomaculatus* were ≥50 mm L_S, with four of them showing the external morphology of sexually active males.

Due to a comparative lack of mature specimens, it was not possible to perform a statistical analysis of sex-specific EOD characteristics. A specimen and 10 unique EOD waveforms are displayed in Fig. 6. A single specimen had a p-POS amplitude below the 1·5% threshold. For a summary of the EOD characteristics see Table V. The EODs of the *P. pallidomaculatus* and *P. cf. pallidomaculatus* resembled each other very much and differed only in two of the measured EOD variables (Fig. 4): the m-POS amplitude and the area of m-NEG. The m-POS amplitude of the *P. cf. pallidomaculatus* EOD was only

TABLE IV. Comparison of *Petrocephalus cf. pallidomaculatus* from the Volta basin and *Petrocephalus pallidomaculatus* from south Benin

	P. cf. pallidomaculatus (n = 52)		*P. pallidomaculatus* (n = 38)	
	Mean ± S.D.	Range	Mean ± S.D.	Range
L_S in mm	52·6 ± 6·1	42·0–69·1	47·8 ± 6·1	38·1–62·5
Body depth, % L_S	29·5 ± 1·4	26·1–32·9	29·8 ± 1·4	26·7–32·5
L_H, % L_S	26·6 ± 1·1	26·0–33·0	30·3 ± 1·3	23·3–33·8
Head width, % L_H	40·1 ± 1·9	38·1–45·8	44·4 ± 2·6	38·5–50·7
Eye diameter, % L_H	26·0 ± 2·5	21·4–31·2	28·1 ± 1·9	24·1–32·1
Snout length, % L_H	16·0 ± 1·9	12·0–21·6	16·3 ± 1·6	12·4–19·4
Base of dorsal fin, % L_S	20·4 ± 1·2	18·3–23·0	19·7 ± 1·0	18·1–21·8
Base of anal fin, % L_S	27·6 ± 1·4	24·0–32·0	26·5 ± 1·0	24·2–28·1
Caudal peduncle depth, % caudal peduncle length	74·1 ± 6·8	57·1–88·7	74·2 ± 3·8	67·5–83·9
Dorsal fin rays	23·7 ± 1·3	21–26	23·5 ± 0·9	21–25
Anal fin rays	31·3 ± 1·1	29–34	30·0 ± 1·0	28–33

L_H, head length; L_S, standard length.

21·1 ± 1·3% (range from 15·0 to 26·0%) of the total EOD amplitude, while it was 25·2 ± 1·8% (range from 22·7 to 29·5%) in *P. pallidomaculatus*. In the two scatter plots of EOD variables (Figs 5 and 7), *P. cf. pallidomaculatus* and *P. pallidomaculatus* always clustered together.

A list of multiple statistical comparisons of several EOD variables among the species of this study are given in Fig. 4. For each variable, a univariate analysis was conducted. All these comparisons were significant ($P < 0·001$). These were then followed by Games–Howell *post hoc* tests. The significance level was set at $\alpha = 0·05$. The results show that almost all variables differed significantly between the *Petrocephalus* species of the Upper Volta basin. Only the EOD duration and the area of m-POS were not different between *P. bovei* and *P. cf. pallidomaculatus* and the area of p-POS between *P. soudanensis* and *P. cf. pallidomaculatus*.

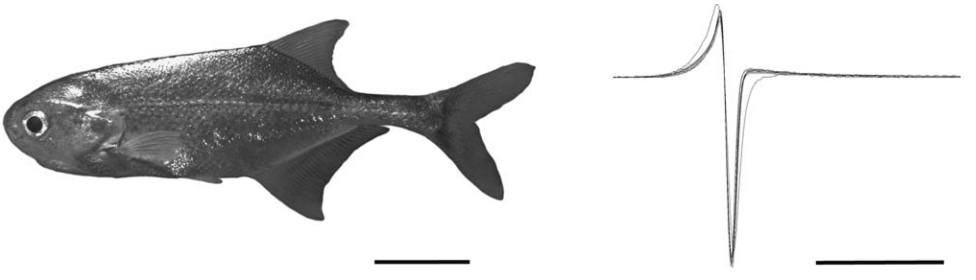

FIG. 6. *Petrocephalus pallidomaculatus* and electric organ discharge (EOD) from the first 10 specimens caught at Hossa at the Ouémé River, Southern Benin. Scale for specimens 10 mm, scale for EOD 100 μs.

TABLE V. Characteristics of 17 electric organ discharges (EOD) from *Petrocephalus pallidomaculatus* from south Benin (see Figs 1 and 2)

Location	*n*	Dur. EOD (μs)		Dur. m-POS		Dur. m-NEG		Dur. p-POS		Amp. m-POS		Amp. p-POS		FFT-peak (Hz)	
		Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
Hossa at Oueme	17	261 ± 39	186–324	106 ± 11	90–130	43 ± 7	36–70	112 ± 42	nd/60–168	25·2 ± 1·8	22·7–29·5	2·9 ± 1·0	0·0–4·3	7983 ± 992	6104–9766

Amp., amplitude of phase in per cent of total EOD amplitude; Dur., duration; FFT, fast Fourier transformation; nd, not detected.

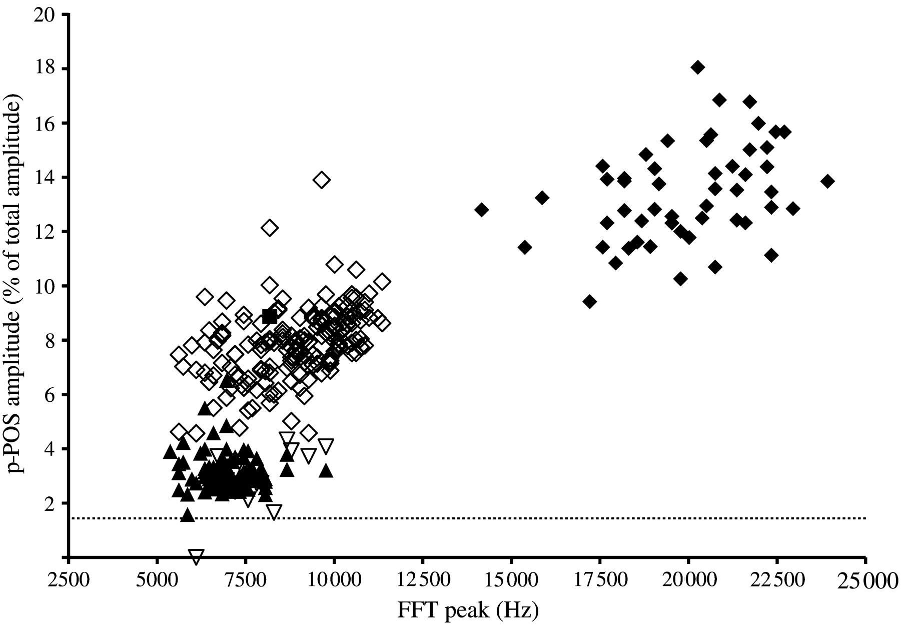

FIG. 7. Scatterplot of the relative amplitudes of p-POS (see Fig. 2) and the peak frequencies of the fast Fourier transformations (FFT) of the electric organ discharge (EOD) of *Petrocephalus bovei* (◇, $n = 168$), *Petrocephalus soudanensis* (◆, $n = 52$), *Petrocephalus bane* (■, $n = 1$) and *Petrocephalus cf. pallidomaculatus* (▲, $n = 94$) from the Upper Volta, and *Petrocephalus pallidomaculatus* (▽, $n = 17$) from the Ouémé. The 1·5% amplitude threshold is displayed as a dotted line.

A comparison of the EOD characteristics of all investigated specimens by PCA (Fig. 8) maps *P. soudanensis* clearly separated from the other species. The minimum polygon clusters of *P. cf. pallidomaculatus* and *P. pallidomaculatus* largely overlap. The single *P. bane* clusters within *P. bovei*, and there is very little overlap between the latter species and *P. cf. pallidomaculatus*. Separate PCAs for different locations always resulted in minimum polygon clusters for the respective species not overlapping. Summarizing all locations within the Pendjari River resulted in separated convex hulls, with exception of *P. bane*, which clustered within *P. bovei*. The first two factors of the PCA explained together 88·9% of the total variance between the species. The most important variables for the loading of these factors were the peak frequency and variables related to p-POS (Fig. 8).

DISCUSSION

THE IDENTITY OF *P. CF. PALLIDOMACULATUS*

From the four *Petrocephalus* species found in the Upper Volta system, the identity of *P. cf. pallidomaculatus* is problematic. *Petrocephalus pallidomaculatus* was first described in 1990 (Bigorne, 1990; Bigorne & Paugy, 1991) based on 55 specimens from the Upper Niger in Mali and Guinea, 64 specimen from the Ouémé in Benin, 14 specimens from the Mono in Togo and a single specimen

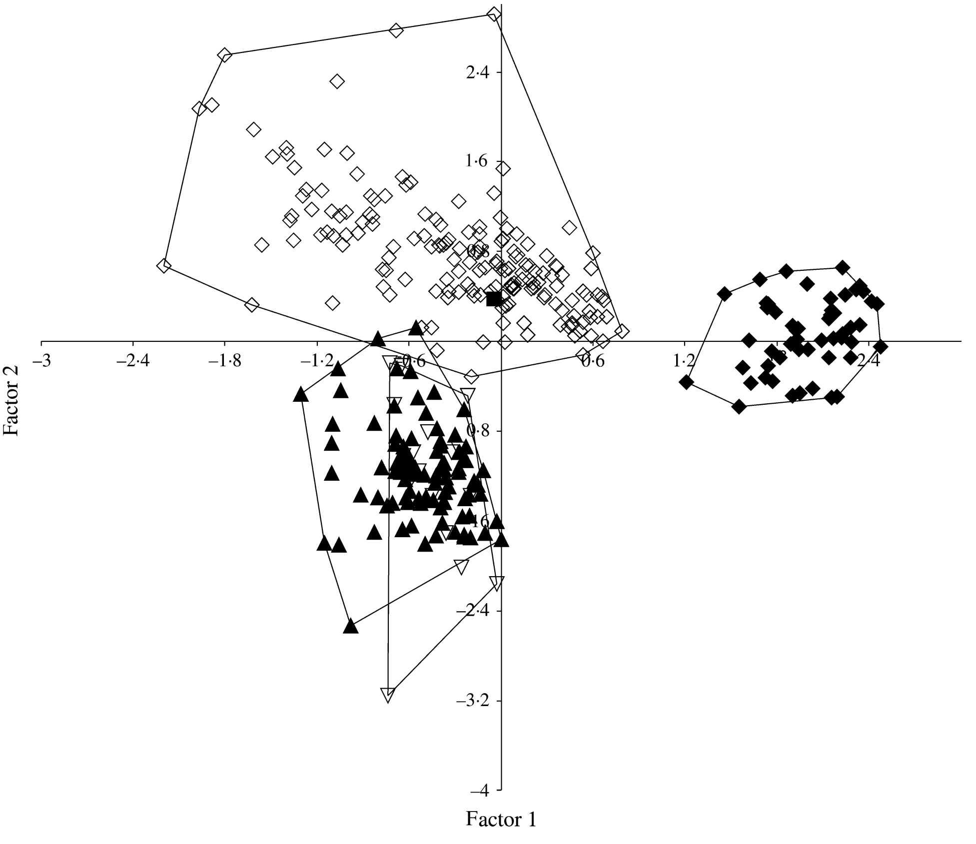

FIG. 8. Plot of the first and second factor axis scores from a principal component analysis (PCA) of electric organ discharges (EOD) from *Petrocephalus* species. Each point represents a single EOD from *P. bovei* (◇, $n = 168$), *P. soudanensis* (◆, $n = 52$), *P. bane* (■, $n = 1$) and *P. cf. pallidomaculatus* (▲, $n = 94$) from the Upper Volta, and *P. pallidomaculatus* (▽, $n = 17$) from the Ouémé. The first factor axis explains 66·6% of the variance in the original data. The EOD variables that load most heavily onto this axis are fast Fourier transformation (FFT) peak (loading +0·445), amplitude of p-POS (+0·385), duration of p-POS (−0·358), duration of m-NEG (−0·343) and area of m-NEG (−0·343) (see Fig. 2). The second principal factor axis explains additional 22·3% of the total variance. The respective variables that load most heavily onto this axis are area of p-POS (+0·732), amplitude of p-POS (0·523) and duration of p-POS (+0·343).

from the Volta system. The last was labelled as coming from the Sabari on the Oti River in Burkina Faso (Bigorne & Paugy, 1991). Sabari is indeed situated at the Oti, but it is located in Ghana, 200 km south of Burkina Faso in agreement with a corresponding 'dot' on the distribution map shown in Bigorne & Paugy (1991). Later, Bigorne (2003) shows two new locations of occurrence, plotted on the distribution map: the Niger Delta in Nigeria, based on specimens deposited in the Musée Royal de l'Afrique Centrale, Tervuren (MRAC), and a second spot in Eastern Burkina Faso in the area of Koupéla. For the latter, it was not possible to corroborate this occurrence, thus raising the possibility that this point was plotted based on the former mistake positioning Sabari in Burkina Faso.

Petrocephalus cf. pallidomaculatus from the Upper Volta does not show any difference from *P. pallidomaculatus* from the Ouémé based on meristics and morphometrics (Table V) and few differences in EOD characteristics (Figs 4, 5 and 7 and Tables III and IV): only the colour pattern is slightly different. Based on these data, both forms probably belong to a single species with slight local differences in colouration. On the other hand, the presence of such a colour pattern is the only diagnostic character given by Bigorne & Paugy (1991) to distinguish *P. pallidomaculatus* from *P. bovei*, except for the 'plan génétique' (genetic level), which these authors do not explain any further. Indeed, *P. bovei* and *P. pallidomaculatus* look similar in size and shape but can be distinguished by eye size and EOD waveform characteristics (Figs 4, 5 and 7). Nevertheless, both species resemble each other, and *P. cf. pallidomaculatus* from the Volta system was probably not distinguished from *P. bovei* by most ichthyologists working in this area.

EOD WAVEFORMS OF *PETROCEPHALUS*

Hopkins (1999*a*) and Sullivan *et al.* (2000) stated that the Petrocephalinae have biphasic EODs. In contrast, this and other studies (Bratton & Kramer, 1988; Kramer, 1997; Kramer & van der Bank, 2000; Lavoué *et al.*, 2004) revealed a triphasic waveform of *Petrocephalus* EODs, although the third phase can be quite small, as for example in *P. pallidomaculatus*. What is called a third phase in this study and by some other authors (Bratton & Kramer, 1988; Kramer, 1997; Kramer & van der Bank, 2000; Lavoué *et al.*, 2004) is regarded as an 'overshoot' by others (Hopkins, 1999*a*; Sullivan *et al.*, 2000). So far there is no substantial difference, but only a nomenclatural disagreement in the evaluation of the EOD of *Petrocephalus*. A real discrepancy arises, however, from Sullivan *et al.*'s (2000) statement that some *Petrocephalus* species do not even have such an 'overshoot'.

The shape of the EOD waveform of *P. bovei* in this study was similar to that reported by Bratton & Kramer (1988) but differed from that shown by Alves-Gomes & Hopkins (1997). The latter authors plot an EOD with almost no p-POS for *P. bovei* caught in the Niger River basin in Mali. Unfortunately, the authors do not state on how many records their results are based. Explanations for the discrepancy between these and the present results could be a confusion of non-coloured *P. pallidomaculatus* with *P. bovei* without noticing the very small p-POS or a geographic variation in the EOD of *P. bovei*. Due to its wide distribution all over West Africa, the Chad region and the Nile River basin (Gosse, 1984), local variations may be possible. Based on the present data this issue cannot be solved.

Mormyrids often have sexually dimorphic EODs with mature males emitting significantly longer discharges than females (Carlson *et al.*, 2000). For *Petrocephalus* spp., such a sexual dimorphism has not yet been clearly shown. While all authors agree on the absence of a sexual EOD dimorphism in *P. bovei* (Bratton & Kramer, 1988; Alves-Gomes & Hopkins, 1997), this is less clear for other species. In *Petrocephalus catostoma* (Günther), Kramer (1997) reports a 'sex difference' (unequal to 'sexual dimorphism') with mature males having distinctly longer EODs than their female conspecifics of the same size. These differences were not, however, statistically significant (Kramer, 1997). For the species treated in the present study, neither sexual dimorphism nor 'sex differences' in the EOD waveform could be found.

SPECIES IDENTIFICATION AND EVOLUTION OF EOD WAVEFORMS

The present study showed that it is possible to distinguish between three sympatric and often syntopically occurring species of *Petrocephalus* (*P. bovei*, *P. soudanensis* and *P. cf. pallidomaculatus*) on the basis of their EODs. For the fourth species, *P. bane*, there are too few data for conclusions, but probably *P. bane* and *P. bovei* from the same locality can also be discriminated on the base of their EODs. The EOD waveforms contain enough information allowing identification of species, especially due to characters from p-POS and peak frequency. Thus, if the fishes have the sensory abilities to extract waveform information, the EOD waveforms would have the potential to serve in species recognition and reproductive isolation in the *Petrocephalus* species from the Upper Volta system. If such EOD waveform discrimination exists, it is probably accomplished by the Knollenorgan pathway (Xu-Friedman & Hopkins, 1999). Arnegard *et al.* (2006) showed recently that the Knollenorgan pathway from sympatric morphs of the *Brienomyrus* complex is able to discriminate between different temporal EOD waveform features. The same mechanism probably exists in *Petrocephalus* species, although their EOD signals are shorter than those of the *Brienomyrus* complex and thus may border on the temporal resolution of Knollenorgans. In any case, the present investigation only tested if the EOD waveforms of the *Petrocephalus* spp. studied differed from each other. If these differences actually serve for species recognition and reproductive barriers, it is not verified. Also, the sequence of pulse intervals (SPI) could be important for species recognition and future studies need to investigate how far EODs and SPIs are really utilized.

When comparing waveforms of *Petrocephalus* EODs reported in the literature, it appears that irrespective of absolute EOD duration, there exist three basic types of EOD waveforms in this genus. Type I has a p-POS of moderate duration and an amplitude of *c.* 6·5–9·5% of the total EOD amplitude. In this study, *P. bovei* and *P. bane* emit type I EODs. Examples from the literature include *P. catostoma* (Kramer, 1997; Kramer & van der Bank, 2000) and *Petrocephalus simus* Sauvage and *Petrocephalus balayi* Sauvage (Lavoué *et al.*, 2004). Type II EODs have a moderate duration and a p-POS amplitude of 2–4% of the total EOD amplitude. Type II EODs occur in *P. cf. pallidomaculatus* (Volta basin) and *P. pallidomaculatus* (Ouémé) in the present study, and in *Petrocephalus wesselsi* Kramer & van der Bank (Kramer & van der Bank, 2000) and *Petrocephalus microphthalmus* Pellegrin (Lavoué *et al.*, 2004). Finally, type III EODs are rather short EODs with a p-POS of *c.* 11·5–14·5% of the total EOD amplitude, as in *P. soudanensis* (this study) and in *Petrocephalus sullivani* Lavoué, Hopkins & Kamdem Toham (Lavoué *et al.*, 2004).

All these types can be easily modelled by an overlay of two Gaussian functions, as proposed by Westby (1984) for *Pollimyrus adspersus* (Günther). According to this model, the EOD waveform of *Petrocephalus* may be a combination of two approximately Gaussian functions, produced by the two faces of the electrocytes of the electric organ, as proposed by Lavoué *et al.* (2004). With only a few changes in the equation, *i.e.* the relative timing between the functions and their slope, it is possible to synthesize any type of *Petrocephalus* EOD (Westby, 1984). Accordingly, it could be that only simple alterations in the nervous excitation pattern of the electric organ occur during evolution, *e.g.* rate of membrane polarization and depolarization or point of time for switching from polarization to depolarization, leading to the different waveform types. For example, by slightly changing the responsiveness of the rostral and caudal electrocyte membranes, it might be possible to delay or advance the generation of the second negative (m-NEG) phase of the EOD. A longer delay would lead to longer duration signals that have almost no p-POS (*P. pallidomaculatus*), while a very short delay of the second negative phase relative to the first positive phase would lead to shorter EODs with a stronger p-POS (*P. soudanensis*).

A recent investigation of the EODs of several sympatric *Petrocephalus* species from one region was performed by Lavoué *et al.* (2004) for the Ogooué River and its neighbouring smaller basins. Their differing EOD waveforms correspond in shape, but not in duration, to the three types found in the present study. The resemblance of the results becomes even more striking when plotting the FFT maximum frequencies and the p-POS amplitudes of the *Petrocephalus* EODs for both studies (Fig. 7): Fig. 7 is very similar to Fig. 3 in Lavoué *et al.* (2004), with the important difference that the total EOD durations in the latter study are about twice as long as in the present findings. This leads to FFT maxima, which are about half the values measured. Nevertheless, the sympatric *Petrocephalus* EODs from the Ogooué River can be divided into the same waveform types I, II and III as in the present study, even if the duration level is doubled at the former location.

The principal resemblance of EOD waveform diversity of sympatric *Petrocephalus* species within different river basins suggests a biological function. In the literature, two reasons for EOD waveform diversity are given: first, EOD waveform is an adaptation to the habitat of the fishes, *i.e.* in different environments certain EOD waveforms may be better suited for orientation and prey detection than others (Kramer & Kuhn, 1993; Alves-Gomes & Hopkins, 1997). Second, EOD waveforms may allow species recognition, thus serving as reproductive isolation mechanism (Moller & Serrier, 1986; Crawford & Hopkins, 1989; Alves-Gomes & Hopkins, 1997; Arnegard *et al.*, 2005). The first reason (habitat specificity) appears not to be convincing for the *Petrocephalus* species from the Upper Volta because all species (except *P. bane*) occurred at least in some places syntopically. Furthermore, habitat alteration during a year is extremely high in this area (rainy and dry season). The second hypothesis (species recognition) thus appears more likely but needs to be tested in future studies. Especially, it has to be tested whether the Knollenorgan system is capable of resolving the differences in waveform between the species that are shown in this study.

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APPENDIX

The following specimens were deposited at the Natural History Museum, London, U.K. *Petrocephalus bovei*: BMNH 2006.7.21.1-9, nine specimens, 34·4–40·9 mm standard length, L_S, Small River at Biakou, Tanguieta, Benin, 26.02.2005; BMNH 2006.7.21.10-38, 29 specimens, 25·9–47·7 mm L_S, Mare Bori, Pendjari National Park, Benin, 27.02.2005; BMNH 2006.7.21.39-60, 22 specimens, 49·1–67·0 mm L_S, Mare Tiabiga, Pendjari National Park, Benin, 12.05.2005.

Petrocephalus pallidomaculatus: BMNH 2006.7.21.61-98, 38 specimens, 38·1–62·5 mm L_S, Hossa at Oueme River, Benin, 12.05.2005.

Petrocephalus cf. pallidomaculatus: BMNH 2006.7.21.99-110, 12 specimens, 41·5–53·8 mm L_S, Mare Tiabiga, Pendjari National Park, Benin, 01.03.2005; BMNH 2006.7.21.111-132, 22 specimens, 40·4–52·4 mm L_S, Pont Arly, Pendjari River, Pendjari National Park, Benin, 02.03.2005; BMNH 2006.7.21.133-184, 52 specimens, 42·0–69·1 mm L_S, Ouessa at Black Volta (= Mou-Houn), Burkina Faso, 06.03.2005; BMNH 2006.7.21.185-187, three specimens, 36·6–64·6 mm L_S, Bougouriba River close to Dan, Burkina Faso, 10.03.2005.

Petrocephalus soudanensis: BMNH 2006.7.21.188-195, eight specimens, 31·0–69·0 mm L_S, Pont Arly, Pendjari River, Pendjari National Park, Benin, 02.03.2005; BMNH 2006.7.21.196-199, four specimens, 44·3–64·4 mm L_S, Bougouriba River close to Dan, Burkina Faso, 10.03.2005.

